PACIFIC SCIENCE Early View

A Quarterly Devoted to the
Biological and Physical Sciences of the Pacific Region

Biology and Impacts of Pacific Island Invasive Species: 8. *Eleutherodactylus planirostris*, the Greenhouse Frog (Anura: Eleutherodactylidae)

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Abstract

The greenhouse frog, *Eleutherodactylus planirostris*, is a direct-developing (i.e., no aquatic stage) frog native to Cuba and the Bahamas. It was introduced to Hawaii via nursery plants in the early 1990s and then subsequently from Hawaii to Guam in 2003. The greenhouse frog is now widespread on five Hawaiian Islands and Guam. Infestations are often overlooked due to the frog's quiet calls, small size, and cryptic behavior, and this likely contributes to its spread. Because the greenhouse frog is an insectivore, introductions may reduce invertebrates. In Hawaii, the greenhouse frog primarily consumes ants, mites, and springtails, and obtains densities of up to 12,500 frogs ha^{-1}. At this density, it is estimated that they can consume up to 129,000 invertebrates ha^{-1} $night^{-1}$. They are a food source for the non-native brown tree snake in Guam and may be a food source for other non-native species. They may also compete with other insectivores for available prey. The greatest direct economic impacts of the invasions are to the nursery trade that must treat infested shipments. Although various control methods have been developed to control frogs in Hawaii, and citric acid, in particular, is effective in reducing greenhouse frogs, the frog's inconspicuous nature often prevents populations from being identified and managed.

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This **early view** paper has been peer-reviewed and accepted for publication in *Pacific Science*. However, it has not been copy-edited nor has it undergone typesetting for *Pacific Science*. The final published paper will look different due to formatting changes, but scientific content will remain the same.

Pacific Science, vol. 66, no. 3, pp. 000-000
November 30, 2011 (Early view)

Official Journal of the Pacific Science Association

Introduction

The greenhouse frog, *Eleutherodactylus planirostris* (Cope 1862), is a direct-developing (i.e., no aquatic stage) frog native to Cuba and the Bahamas; it has established breeding populations on five islands in Hawaii and Guam, as well as the US mainland and at least four Caribbean localities (Kraus 2009). In general, its invasions have not been well studied, even though the greenhouse frog is one of the most successful amphibian invaders (Bomford et al. 2009). This may be because the species is not often noticed, due to its small size (< 30 mm), inconspicuous advertisement call (Kraus and Campbell 2002), and easily overlooked soil-deposited eggs. Because the greenhouse frog does not require standing water for transport, establishment, or persistence, additional inadvertent translocations in the Pacific region are probable (Christy et al. 2007a).

The introduction of non-native *Eleutherodactylus* has affected the nursery trade in Hawaii. In addition, the non-native Puerto Rican coqui, *E. coqui*, can negatively impact Hawaiian ecosystems through predation on invertebrates and by altering nutrient cycles (Beard 2007, Sin et al. 2008, Choi and Beard in press). There may be similar impacts from the greenhouse frog. High densities of the greenhouse frog may also facilitate the establishment and spread of other non-native species in the Pacific, in particular that of the brown treesnake, *Boiga irregularis* (Mathies et al. in press). Thus, it is important to know how the greenhouse frog impacts Pacific Islands, and the state of management of its invasion.

NAME

Eleutherodactylus planirostris (Cope, 1862)

Phylum Chordata, class Amphibia, order Anura, family Eleutherodactylidae

Synonym: *Hylodes planirostris* Cope 1862, *Lithodytes* (= *Eleutherodactylus*) *ricordii* Cope, 1875, *Eleutherodactylus ricordii planirostris* Shreve, 1945, *Eleutherodactylus planirostris planirostris* Schwartz, 1965.

As the Latin meaning of the genus name implies, *Eleutherodactylus* (Dumeril & Bibron) frogs have individual (non-webbed) fingers and toes. The name *planirostris* comes from the Latin "rostrum" (snout) and "planum" (level, flat). There are 185 species in the genus, distributed throughout the West Indies, the southern United States, Mexico, Belize, and Guatemala (Hedges et al. 2008). Hedges et al. (2008) suggested that *E. \planirostris* should be classified in the subgenus *Euhyas* (Fitzinger) because of differences in liver shape, no external vocal sac, and more terrestrial behavior than the more arboreal species classified in the subgenus *Eleutherodactylus*. The family-level classification of this group, currently Eleutherodactylidae, has been highly unstable in the last decade; it was routinely placed in Leptodactylidae prior to recent molecular assessments of frog phylogeny (Hedges et al. 2008). Commonly known as the greenhouse frog, it is often found in plant nurseries, gardens, and greenhouses (Schwartz and Henderson 1991). Previous common names of the greenhouse frog that are no longer in use include the Ricord's frog, cricket toad, Bahaman tree frog, and pink-snouted frog (Wright and Wright 1949).

DESCRIPTION AND ACCOUNT OF VARIATION

Species Description

A small species of *Eleutherodactylus*, the greenhouse frog is sexually dimorphic. On the island of Hawaii, maximum snout-vent length (SVL) for females was 27 mm (mean = 22, n = 176) and 21 mm (mean = 17, n = 100) for males across 10 sites, with females 30 to 40% longer than males (Olson and Beard in press). These sizes are similar to those in their native Cuba and non-native

Florida, where females have a maximum SVL range of 26.5-28 mm and males a maximum SVL range of 17.5-21 mm (Schwartz 1974, Meshaka et al. 2004).

There are two basic color phases: (1) a mottled tan and brown phase (Figure 1), and (2) a mottled tan and brown phase with two yellow dorsolateral stripes extending from the eye along the length of the body (Figure 2) (Lynn 1940). The mottled pattern is recessive to the dominant striped pattern, and in Cuba, there is a 3:1 ratio of striped to mottled individuals (Goin 1947). A population from Gainesville, Florida (USA) exhibited a 1:1 ratio, which may have been a result of a bottleneck effect (Goin 1947) or selective pressure (Woolbright and Stewart 2008). Only mottled individuals were found in recent studies across the islands of Hawaii, Lanai, and Maui (Olson and Beard in press, Choi unpubl. data). In museum specimens from Hawaii, the dominant pattern was also mottled, with only 14% exhibiting striped patterns (12 out of 155 specimens) and all striped individuals were collected from Oahu (Bishop Museum, Honolulu, Hawaii, USA, Fred Kraus pers. comm.). Hundreds of greenhouse frogs have been collected across Guam, and only mottled frogs have been found (Diane Vice, unpubl. data).

Distinguishing Features

In Cuba, 85% of the native frog species are in the *Eleutherodactylus* genus (55 out of 66 species). The greenhouse frog was originally identified as *E. ricordii* and was split when the two species were found syntopic in eastern Cuba (Schwartz 1974), thus several early references to Florida populations state *E. ricordii* while only *E. planirostris* was introduced. Two species, *E. goini* and *E. casparii*, were at one time considered subspecies of *E. planirostris* (Schwartz 1974, Díaz and Cádiz 2008).

Of the frogs introduced to Hawaii, the greenhouse frog most resembles *E. coqui*, the Puerto Rican coqui frog. Features that distinguish the coqui are its light tan color, golden eyes, wider snout, and large toe pads (Beard et al. 2009). The coqui is also larger than the greenhouse frog, with a maximum SVL for females of 49 mm and for males of 39 mm (Beard et al. 2009). Most notably, the breeding call is different. The greenhouse frog produces short, irregular, soft chirps (Schwartz 1974) with sound pressure levels around 35-45 dB at 0.5 m (K. Beard, unpubl. data), which are often mistaken for a cricket or bird, while the coqui produces a loud, two note "ko-kee" call that can reach sound pressure levels of 80–90 dB at 0.5 m (Beard and Pitt 2005). In Guam, there are no other *Eleutherodactylus* species, but it may be confused with non-native newly metamorphosed cane/marine toads (*Bufo marinus*), which also have been introduced to Hawaii; however, the greenhouse frog lacks the cane toad's large, conspicuous parotid glands.

Combinations of physical traits important for identifying the greenhouse frog include:

(1) Size: SVL for reproductive males: 14 to 21 mm; gravid females: 17 to 27 mm in Hawaii (Olson and Beard in press).

(2) Body color: venter is white to light gray and dorsal is tan-pink to dark reddish-brown (Ashton and Ashton 1988, Bartlett and Bartlett 2006). There is a dark S-shaped line from top of tympanum to arm insertion (Wright and Wright 1949).

(3) Body shape: head as broad as body, snout truncated and extending slightly beyond the lower jaw (Wright and Wright 1949).

(4) Eye color: black pupil with a reddish iris (Wright and Wright 1949).

(5) Foot features: toes are long, slender, lack webbing and have very small, terminal disks (Wright and Wright 1949).

(6) Tympanum: white or coral red, approximately half the size of the eye (Wright and Wright 1949).

ECONOMIC IMPORTANCE AND ENVIRONMENTAL IMPACTS

Detrimental Aspects

Greenhouse frogs and their eggs frequently move unintentionally with plants or landscape materials, and therefore may affect industries involved with this movement, such as the floriculture industry, which is the largest single agricultural commodity for the state of Hawaii (HASS 2005). In Hawaii, inter-island and international plant shipments are inspected, certified as pest-free, and potentially treated for frogs prior to shipment. Infested plant shipments may be refused entry or destroyed (Raloff 2003). Treatment of infested plants increases shipment costs and may also reduce trade. Although there is no information available on the amount nursery owners spend to control greenhouse frogs, treatment can be necessary to maintain pest-free status, and some nurseries treat plant shipments prior to inter-island and international transport.

In addition to economical impacts to agricultural industries, several resorts in Hawaii have attempted to manage greenhouse frogs because they are found in swimming pools and irrigation boxes; and large populations may similarly affect homeowners (W. Pitt, unpubl. data). Although government funds have not specifically been allocated to target greenhouse frogs, in Hawaii, county, state, and federal governments have incurred costs to control coqui frogs. Greenhouse frog populations are probably indirectly controlled at sites targeted for coqui eradication and control, which cost public agencies $4 million in 2006, but expenditures have declined in recent years (Anonymous 2010).

Beneficial Aspects

In general, there is little concern over the spread of greenhouse frogs (Kraus and Campbell 2002). Because of its quiet call, many residents in Hawaii do not consider the frog a nuisance, and some have expressed preferences for the greenhouse frog over the coqui (C. Olson, pers. obs.). Some residents find the frogs and their calls pleasing, and frogs have been intentionally moved to gardens or homes. Some who move frogs incorrectly believe that all frogs control harmful invertebrates, such as mosquitoes and termites (Fullington 2001, Singer 2001). A diet study of the greenhouse frog conducted in Hawaii indicates this is unlikely; only two mosquitoes and no termites were found out of 7,494 identified prey items (Olson and Beard in press).

Ambivalence and inability to detect new infestations may facilitate the spread of greenhouse frogs. For example, both the coqui and greenhouse frog were introduced to Guam in 2003 (Christy et al. 2007b). The coqui was quickly eradicated but the greenhouse frog established and spread throughout the island with little alarm (Daniel Vice, pers. comm.). This may have occurred because the coqui was easier to detect, because of its louder call, while populations were still small enough to treat, but also may have occurred because there was less concern about the greenhouse frog.

Regulatory Aspects

In Hawaii, all frogs (they are all non-native) are listed as State Injurious Species and it is illegal to transport or release frogs into the wild. The requirement to treat plants prior to shipment is required primarily to combat coqui frogs, but the presence of any frog in a shipment would trigger legal requirements to restrict movement (Hawaiʻi Department of Agriculture 150A-2, Hawaiʻi Revised Statutes). Plant shipments from Hawaii to Guam, the continental United States, and other countries require a phytosanitary certificate that certifies shipments are pest-free and shipments may be inspected visually or by listening for calling frogs during the daytime. However, this often does little to prevent movement of greenhouse frogs or their eggs, because the small frogs and their eggs are not easily detected and the soft nighttime chirps of calling males may not be heard (Keevin Minami, pers. comm.). Further spread could be reduced if all shipments were treated whether or not frogs or eggs are detected.

Environmental Impacts

Because the greenhouse frog is an insectivore (Goin 1947, Stewart 1977), their greatest threat to Pacific ecosystems is to the invertebrate communities. To determine impacts to invertebrate communities, the greenhouse frog diet was determined at 10 sites on the island of Hawaii (Olson and Beard in press). Greenhouse frogs were found to primarily consume leaf litter invertebrates and were estimated to consume up to 129,000 invertebrates ha^{-1} $night^{-1}$ (Olson and Beard in press). Because the study did not identify stomach contents to species, it is unknown how much of the total diet was comprised of native species. A significant portion of their diet included mites (19% out of the total number of all items consumed), springtails (17%), spiders (3%), beetles (2%), flies (2%), and booklice (2%), all of which are invertebrate orders that contain native species found in Hawaii (Olson and Beard in press). Overall, 42% of the species identified in the diet were non-native ants (32%), isopods (8%) and amphipods (1%) (Olson and Beard in press). All ant species are non-native to Hawaii, and species identified in the diet included the big-headed ant (*Pheidole megacephala*), the Argentine ant (*Linepithema humile*), and the yellow crazy ant (*Anoplolepis gracilipes*). Studies indicate that these ant species, in particular, consume and negatively impact native invertebrates (Krushelnycky et al. 2005). Thus, the frog introduction may indirectly benefit these native invertebrates.

Native fauna may be threatened by introduced *Eleutherodactylus* through pathways besides predation. It was hypothesized that the coqui may compete with native insectivores, such as endemic birds, for prey because of its potential to invade high elevation forests in Hawaii (Kraus et al. 1999, Beard and Pitt 2005). Kraus et al. (1999) considered this to be of less concern for the greenhouse frog because 1) at the time, greenhouse frogs were only found in lower elevations, and thus thought less likely to impact native invertebrates and their native predators, which primarily reside in high elevation forests, and 2) because the greenhouse frog forages in the leaf litter, and thus are less likely to compete with native birds that forage in the canopy. However, it has since been found that the greenhouse frog may invade higher elevations than the coqui (Olson et al. in press). Furthermore, diet studies of the coqui and greenhouse frog indicate that both species predominantly consume leaf litter invertebrates in Hawaii (Beard 2007, Olson and Beard in press), but no specific study has been conducted to determine if either species competes with native insectivores in Hawaii.

It was also hypothesized that large populations of introduced frogs in Hawaii may facilitate the spread of other invasive species by providing an abundant prey source that does not naturally occur (Kraus et al. 1999). Beard and Pitt (2006) conducted diet analysis on mongoose and rat on the eastern side of the island of Hawaii, and found that *Eleutherodactylus* made up a small or negligible part of their diets. In Guam, another invasive species, the brown treesnake, preys on introduced greenhouse frogs (Mathies et al. in press); although it has not yet been determined their percentage in brown treesnake diets. This suggests that if the brown treesnake is introduced to Hawaii, it may use the greenhouse frog as a prey source, which may facilitate the snake's establishment and spread (Mathies et al. in press).

Greenhouse frogs may also impact ecosystem processes, such as nutrient cycling. For example, many invertebrates that the greenhouse frog consumes play important roles in ecosystem processes, such as decomposition of plant material. Sin et al. (2008) found that herbivory rates were lower, and plant growth and leaf litter decomposition rates were higher in Hawaiian sites with than without coqui because of coqui excrement rather than changes to the invertebrate community. Similar effects may occur at sites invaded by the greenhouse frog either because of changes in invertebrate community or other pathways.

GEOGRAPHIC DISTRIBUTION

The native range of the greenhouse frog comprises several islands in the Caribbean (Heinicke et al. 2011). The greenhouse frog is found island-wide on Cuba, except at the highest elevations (1,100 m), with a maximum elevation of 720 m (Díaz and Cádiz 2008), on the islands of Little Bahama Bank, South Bimini, New Providence, and Eleuthera in the Bahamas (Schwartz and Henderson 1991), and on the islands of Grand Cayman and Cayman Brac in the Caymans (Seidel and Franz 1994). It has now spread to several localities outside of its native range throughout the southeastern United States and Caribbean (Table 1). The most likely pathway for initial introduction to these new areas was via cargo or the nursery trade (Stewart 1977, Wilson and Porras 1983).

The first record of the greenhouse frog in the Pacific basin is from the island of Hawaii in 1994, although initial introduction may have occurred at an earlier date (Kraus and Campbell 2002). It is thought to have arrived via nursery plants (Kraus et al. 1999), possibly from Florida. This is inferred because the greenhouse frog first appeared in nurseries that imported plants from Florida, and it had relatively abundant populations in Florida nurseries around the time of introduction. It was particularly abundant in nurseries raising *Dracaena* species (Kraus et al. 1999). The greenhouse frog was then introduced to Guam from Hawaii via the nursery trade in 2003 (Christy et al. 2007b).

The greenhouse frog is now present on the islands of Hawaii (Will Pitt, pers. comm.), Maui (Adam Radford, pers. comm.), Oahu (Katie Swift, pers. comm.) Kauai (Keren Gunderson, pers. comm.), and Lanai (Figure 3). The striped morph found on Oahu (mentioned above) may reflect a separate introduction on that island (O'Neill and Beard 2010, Peacock et al. 2009). Frogs were initially found in four localities on Guam: Tumon, Tamuning, Mangilao, and Manengon (Christy et al. 2007a), and have rapidly spread to the entire island (Diane Vice unpubl. data). A systematic presence/absence study sampled every 2 km on the major network on the island of Hawaii in 2009 (Olson et al. in press) found males calling at 62 (14%) of the 446 points sampled. Occupancy modeling showed that population detection probabilities were low (< 0.3), but three repeated visits improved detection to > 0.7 (Olson et al. in press).

It may be possible to determine genetically if Pacific greenhouse frogs came from Cuba or some area of its introduced range, such as Florida. Studies indicate that greenhouse frogs in Florida and Hawaii originated from an area in western Cuba, and are distinct from populations found in eastern Cuba, the Bahamas, and the Caymans, and other introduced populations in the Caribbean (Heinicke et al. 2011). In addition, genetic diversity is lower in Florida than in source populations (Heinicke et al. 2011).

HABITAT

Climatic requirements and limitations

Studies on climate requirements of the greenhouse frog indicate that predominantly, the frog has established populations in non-native ranges with similar mean annual and maximum warmest-month temperatures to Cuba (Bomford et al. 2009, Rödder and Lötters 2010). However, it is found in areas with seasonal daily minimum temperatures as low as 4 to 8°C in the southeastern United States (Wray and Owen 1999, Tuberville et al. 2005), and it has been suggested that long-term residence in the Florida Keys may have allowed the greenhouse frog to evolve physiological and/or behavioral adaptations to cope with colder temperatures (Bomford et al. 2009, Heinicke et al. 2011). One study suggests that greenhouse frogs in Hawaii may be limited to areas with mean annual temperatures > 20°C; however, this may reflect its recent introduction, and the species may still spread to cooler areas (Rödder and Lötters 2010).

The greenhouse frog is not found on the highest peaks in Cuba (1,100 m) (Díaz and Cádiz 2008) or Jamaica (2,200 m) where greenhouse frogs are found only from sea level to 600 m (Stewart and Martin 1980). The USA continental range is limited to the southeastern coastal lowlands with an elevation < 200 m. In Hawaii, greenhouse frogs were detected at an elevation of 1,115 m (Olson et al. in press). There may be suitable habitat types in Hawaii above 1,115 m, although temperatures and precipitation decline at higher elevations (Price 1983).

Ecosystem and community types invaded

In its native range, the greenhouse frog is common and well adapted to a wide diversity of habitats, including wet and dry forests, coastal and mountainous areas, rivers, streambeds, caves, rocky outcrops, gardens, and houses (Garrido and Schwartz 1968, Díaz and Cádiz 2008). In Florida, the greenhouse frog is common in wet and dry forests, open grasslands, coastal areas, and scrub habitats (Enge 1997, Meshaka et al. 2004). In Jamaica, it is most often found in drier habitats, such as open grasslands and scrub, as well as lawns, pastures, and roadsides (Stewart and Martin 1980).

Most populations in Hawaii are found in lowland (0–500 m) habitats. Populations have become established along roadsides, and in macadamia nut orchards, nurseries, pastures, residential gardens, resort areas, state forests, and state parks (Olson 2011). Most of the invaded habitats are dominated by non-native plants, however, populations have also been found in native shrublands and forests dominated by the native o'hia tree, *Metrosideros polymorpha* (Olson et al. in press). In Guam, the greenhouse frog has invaded both urbanized and forested areas, including residential gardens and secondary scrub-forests (Bjorn Lardner, pers. comm.).

Habitat resource requirements and limitations

The greenhouse frog is typically found on the forest floor (Olson and Beard in press) and up to 2 m off of the ground (Duellman and Schwartz 1958, Stewart and Martin 1980). In Cuba, the greenhouse frog is often found in the leaf litter, under rocks, and in rock crevices at the mouth of caves (Garrido and Schwartz 1968). It is common in open grassy areas in Jamaica (Stewart and Martin 1980). In Florida, the greenhouse frog is found under rocks, fallen branches, and leaf litter, and in low growing bromeliads and gopher tortoise burrows, as well as burrowing into moist soil (Goin 1947, Lips 1991, Neill 1951, Schwartz and Henderson 1991). In Hawaii, it is found predominantly in the leaf litter as well as under man-made objects (i.e. flower pots, water meters, and tarps), rocks, and inside lava tubes (Olson and Beard in press). The use of daytime retreat sites on or below the forest floor has been documented in Jamaica, Florida, and Hawaii (Goin 1947, Stewart 1977, Olson and Beard in press).

Although there are numerous descriptions of its habitat, there have been no studies investigating factors that limit the greenhouse frog. Overcast or rainy sky conditions are important factors in call activity (Meshaka and Layne 2005, Olson et al. in press), thus precipitation may be an important factor limiting their distribution. Humidity is an important variable for egg development and hatching success (Goin 1947), although the greenhouse frog has higher tolerance for drier conditions than other *Eleutherodactylus* species (Pough et al. 1977). In Cuba and Florida, where there is a distinct wet and dry season, frogs breed more during the wet season (Meshaka and Layne 2005, Díaz and Cádiz 2008), and it is possible that the greenhouse frog has a breeding period limited to a wet season in Hawaii as well (Olson et al. in press).

PHYSIOLOGY AND GROWTH

Based on a study of greenhouse frogs in Florida, minimum body size for breeding males is 15.0 mm SVL and 19.5 mm for breeding females, and they reach sexual maturity after one year (Goin 1947). Eggs are laid individually in or under moist soil, or under fallen leaves or rocks and unlike other members of the genus, there is no guarding of the eggs. Clutch size ranges from 3-26 eggs (n = 104 clutches), with a mean of 16 (Goin 1947). In Hawaii, clutches were found inside irrigation boxes with a mean number of eggs of 10.3 (n=3, K. Beard, unpubl. data).

Like other *Eleutherodactylus*, fertilized eggs undergo direct development, meaning there is no free-living tadpole phase and complete metamorphosis occurs within the egg with young hatching as tiny froglets (Goin 1947). Eggs consist of three layers outside the vitelline membrane and are 5-6 mm in diameter at the time of hatching (Goin 1947). Eggs require 100% humidity to hatch and can be submerged in water for a period of up to 25 days and still remain viable (Goin 1947). Eggs hatch 13-20 days after deposition and newly emerged hatchling are 4.3-5.7 mm SVL (Goin 1947, Lazell 1989). Hatchlings have a small-spined tooth used to rupture the egg, and a reduced tail, both which detach soon after hatching (Goin 1947). Newly emerged hatchlings have the same stripe patterns as adults. One frog in captivity gained four times its original body mass and measured 6.9 mm SVL 30 days after hatching (Goin 1947).

The greenhouse frog has a high tolerance for warm and dry conditions compared to other *Eleutherodactylus* species. One study from Jamaica conducted on two species of native and two species of introduced frogs (including the greenhouse frog) indicated that both introduced species acclimated to and survived longer in higher temperatures than the native species (Pough et al. 1977). The preferred temperature of the greenhouse frog was 27.3 ± 0.66°C, with its critical maximum temperature ranging from 36.4 to 41.8°C (acclimated to 20°C: mean = 38.7 ± 0.38°C, range = 36.4–40.0 °C; acclimated to 30°C: mean = 40.5 ± 0.35°C, range = 39.0–41.8°C).

Critical water loss was at 34.9% ± 0.004 of initial body weight in 40-50% relative humidity (RH), significantly higher than the critical water loss of the native species (24-27% of initial body weight).

REPRODUCTION AND POPULATION DYNAMICS

The breeding season in Cuba is April through January (Meshaka and Layne 2005). In Florida, the breeding season is typically April to early September (Goin 1947, Meshaka and Layne 2005). It is unclear if the greenhouse frog has a distinct breeding season in Hawaii and Guam.

Eleutherodactylus reach a calling peak at night between 1830-0500, but call frequency and duration vary by species (Drewry and Rand 1983). There is no information available on the calling times for the greenhouse frog (Goin 1947). Meshaka and Layne (2005) found that calling in central Florida most frequently took place when air temperature was 23-30°C and RH was 84-100%. Males call from the ground or on vegetation under 1 m in height (Díaz and Cádiz 2008). In Hawaii, males call from under debris and stone fences, as well as from subterranean lava tubes (Olson 2011).

Greenhouse frog density was estimated in a macadamia nut orchard on the eastern side of the island of Hawaii in June 2009 using mark-recapture techniques of adult frogs in a 50 x 50 m plot (Olson and Beard in press). Over seven nights, 651 adults were captured and densities were estimated at 4,564 (4,148-5,101, 95% CI) frogs ha^{-1}. Multiplying this estimate by the preadult to adult ratio of 1.7, it was estimated that the total population density was 12,522 frogs ha^{-1} (Olson and Beard in press). Mark recapture methods were also used to estimate densities at two additional sites in natural areas on the eastern side of the island of Hawaii in January 2010, with estimates of 2,400 (1,720-3,760, 95% CI) and 5,300 (3,728-8,048, 95% CI) frogs ha^{-1} (C. Olson, unpubl. data).

Greenhouse frogs often use coconut husk piles as diurnal retreats in Jamaica. A husk pile removal study was conducted at four sites in northern Jamaica, and the highest density site was estimated to have 4,635 frogs ha^{-1} (including two native and two non-native species) (Stewart and Martin 1980). Overall abundance of frogs in husk piles was higher in the dry season than the wet season for all species. Greenhouse frog abundance was lower in husk piles dominated by the native frog species, and higher in the coastal sites than the upland sites.

RESPONSE TO MANAGEMENT

Chemical control

Most control options for greenhouse frogs were developed for coqui frogs. For example, chemical controls used to control coquis over large areas in Hawaii (Tuttle et al. 2008) and are equally effective against greenhouse frogs (Pitt and Sin 2004a). Currently, only citric acid can be used legally to control *Eleutherodactylus* in Hawaii, although several other chemicals have been identified as effective frog toxicants (Campbell 2001, Pitt and Sin 2004b, Pitt and Doratt 2005, Pitt and Doratt 2008). For example, hydrated lime is effective and was registered as a frog toxicant from 2005-2008. Citric acid is exempt from the requirements of FIFRA by regulation (40 CFR Section 152.25) because it is classified as a minimum risk pesticide. A 16% citric acid solution is 100% effective for greenhouse frogs in the laboratory and is effective in the field (Pitt and Sin 2004a).

Few control efforts have been directed exclusively at greenhouse frogs. In 2003, we evaluated the ability to control greenhouse frogs at five Kauai resorts over a 5 month period (W. Pitt, unpubl. data). Greenhouse frogs are often found in irrigation boxes used for landscape watering at resorts with arid landscapes. We evaluated the immediate and long-term effects of control on frog abundance in irrigation boxes. A 16% citric acid solution was applied bimonthly to infested irrigation boxes. As expected, frogs reinvaded irrigation boxes because citric acid does not have long-term residual effects on frogs (Pitt and Sin 2004a). The number of irrigation boxes at each resort varied from 33−411 ($\bar{x}$ = 185). The application removed all frogs from 91% of irrigation boxes within 24 hours. After 5 months of treatments, 67% fewer irrigation boxes were infested.

Mechanical Control

Mechanical control techniques evaluated for coqui frogs may have similar effects on greenhouse frogs. These methods are directed toward nursery operations, quarantine areas, or residential areas. Hot water spray or vapor treatments are commonly used to treat plant shipments for a variety of pests. Hot water sprayed on plants at either 45 ºC for 1 minute or 39 ºC for 5 minutes was effective against adult coqui frogs (Hara et al. 2010) and similar results are expected for greenhouse frogs, considering their similar thermal tolerances (Pough et al. 1977). Native habitat management, such as leaf litter removal, may reduce frog abundance and the likelihood they will move into an area. Hand capture of coqui frogs is effective when few frogs are present (Beard et al. 2009), but may be more difficult with the more cryptic and harder to catch greenhouse frog. Traps and barriers developed for coquis (Figure 4) have not been tested to determine their effectiveness on greenhouse frogs, although barriers may be equally effective against both species.

NATURAL ENEMIES

In the Caribbean, three racer snakes (*Cubophis canterigerus* on Cuba, *C. caymanus* on Grand Cayman, and *C. vudii* in the Bahamas) and the Cuban treefrog (*Osteopilus septentrionalis*) are predators of greenhouse frogs (Meshaka 1996, Henderson and Powell 2009). Other predators of

Eleutherodactylus species in the Caribbean include invertebrates, frogs, lizards, snakes, birds, and mammals (Henderson and Powell 1999). The ringneck snake (*Diadophis punctatus*), a small (8–38 cm) fossorial species, is a predator in Florida (Wilson and Porras 1983, Lazell 1989). In Guam, the invasive brown tree snake consumes greenhouse frogs (Mathies et al in press). There are no records of Hawaiian species consuming greenhouse frogs. Documented parasites in Cuba include nematodes (Henderson and Powell 2009).

Biological control or the release of organisms to combat the frog likely will have little success in significantly reducing populations and could have many unintended consequences. In many areas, greenhouse frogs are abundant in the presence of numerous predators, parasites, and competitors (Henderson and Powell 2009). For example, brown treesnakes are extremely abundant on Guam and prey on greenhouse frogs; however, frogs continue to spread across the island despite predation pressure (Rodda and Savige 2007, Mathies et al. in press).

Pathogens have a low potential for controlling greenhouse frogs in Hawaii primarily because viruses and diseases are most effective when applied to small populations of species with low reproductive capacity (Brauer and Castillo-Chavez 2001, Daszak et al. 2003). Additionally, most major frog diseases infect tadpole stages and greenhouse frogs would be less affected (Daszak et al. 2003). One disease organism that has been implicated in frog population declines worldwide, the chytrid fungus, is already established in frog populations in Hawaii (Beard and O'Neill 2005). Although there are no native frogs in Hawaii and thus none at risk of infection, there is a chance that a frog infected with a disease could be transported to other states or countries. Thus, releasing a disease organism may affect frog populations elsewhere and could restrict trade.

PROGNOSIS

Greenhouse frogs are widespread in Hawaii and Guam. Control efforts on Hawaii are targeted toward the coqui frog, and there have been no efforts to control the greenhouse frog on Guam; thus, it is unlikely they will be controlled with current methods. Many alternative control measures have been evaluated and found to have low probability of success, including biological control, sterilization, and pathogen release. The best method to control greenhouse frogs is to reduce their spread to new areas with good management techniques, such as inspecting cargo and plant materials, treating plant materials with citric acid solution or hot water, using barriers, and not transporting material that is known to be infested.

Acknowledgments

Support for this research came from the Jack H. Berryman Institute and the Ecology Center at Utah State University. Thanks to F. Kraus, A. Radford, C. Arnott, E. Kalnicky, and R. Choi for providing Hawaii locations. Research was conducted under IACUC Protocol #1402 and the following State of Hawaii permits: Injurious Wildlife Export, and DLNR/DSP Scientific Research, DLNR/ DOFAW Access to Land and Native Invertebrate.

Table 1

Nonnative Distribution of the Greenhouse Frog

Location	Approximate date of first known occurrence	Additional info and references
North America		
United States		
Florida		Widespread throughout the peninsula in human-altered and natural habitats; possibly introduced naturally, such as on driftwood (Goin 1947, Meshaka et al. 2004, Heinicke et al. 2011)
Florida Keys	1863	
Miami	1899	
Gainesville	1933	
Tampa	1938	
Jacksonville	1943	
Louisiana	1975	First record is from a city park in New Orleans; currently found in 10 parishes in the southern part of the state (Meshaka et al. 2009)
Alabama	1982	Found in Baldwin County (Carey 1982)
Georgia	1998	Found in five counties in the southern part of the state (Jensen et al. 2008)
Oklahoma	2000	One population found in a tropical building of Tulsa Zoo (Somma 2010)
Mississippi	2003	Found in the city of Gulfport (Dinsmore 2004).
Veracruz, Mexico	1974	Schwartz 1974
Caribbean Islands		
Jamaica	1937	Found throughout the island, except Hellshire Hills, and the Portland Ridge Peninsula (Hedges 1999)
Grenada	1999	Kraus et al. 1999
Caicos Islands	Unknown	North Caicos Island (Schwartz and Henderson 1991)
Miskito Cays	Unknown	Heinicke et al. 2011
Pacific Islands		
Hawaii	1994	Kraus and Campbell 2002
Guam	2003	Christy et al. 2007a

Figure 1. Photograph of adult female taken in Hawaii showing mottled color phase. Photo: Christina A. Olson.

Figure 2. Photograph of a recently hatched juvenile from Florida (Sarasota County) showing size and striped color phase. Photo: Christina A. Olson.

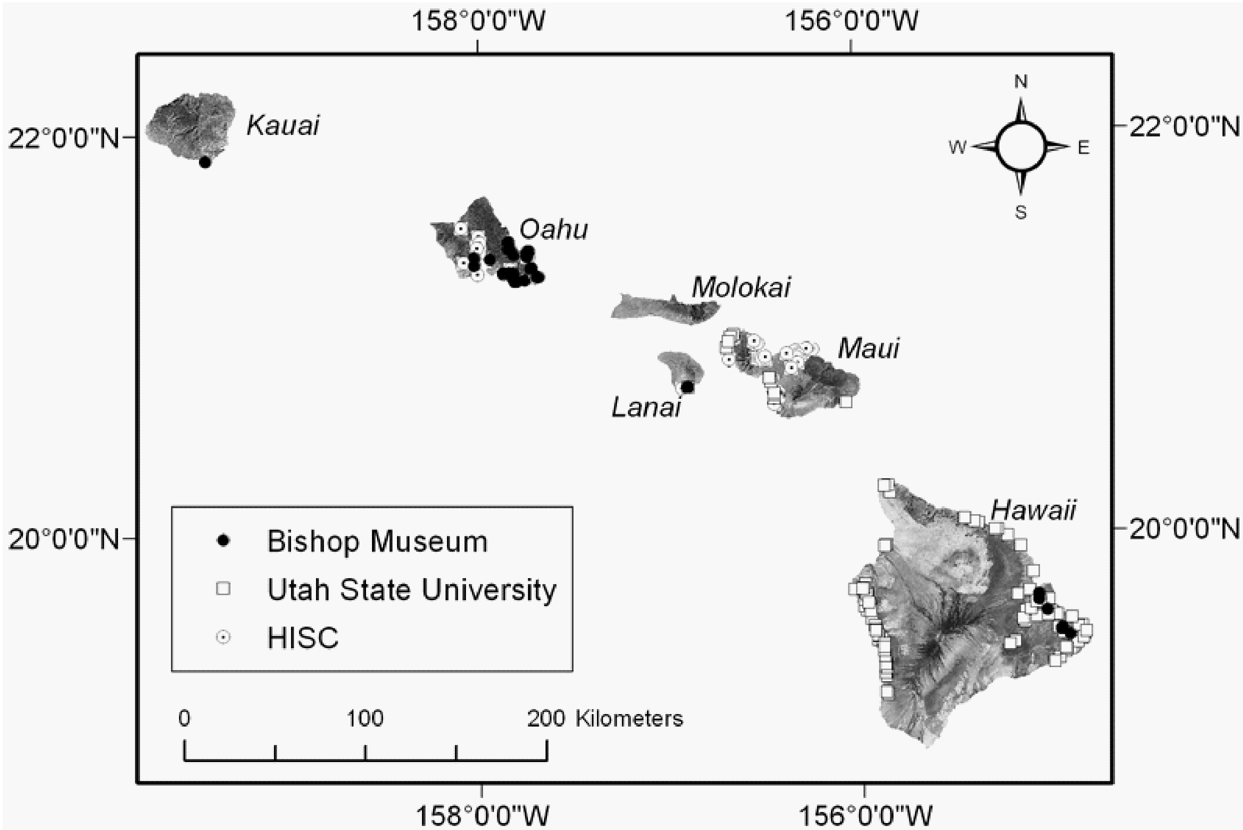

Figure 3. Map of reported locations of *Eleutherodactylus planirostris* on the islands of Hawaii, Kauai, Lanai, Maui, and Oahu including records from the Bishop Museum, Honolulu, HI, USA, Utah State University 2008-2010, and the Hawaii Invasive Species Council (HISC). (Source: Landsat imagery - http://hawaii.gov/dbedt/gis/).

Figure 4. Photograph of a fine mesh frog barrier attached to chain link fence. The frog barrier is 1 m high with the bottom apron buried under gravel and an upper lip extending 25 cm out from the barrier at a 90° angle. Photo: William C. Pitt.

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